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Conditions for view invariance in the neural response to visual symmetry

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Abstract

Symmetry detection is slow when patterns are distorted by perspective, perhaps due to a time-consuming normalization process, or because discrimination relies on remaining weaker regularities in the retinal image. Participants viewed symmetrical or random dot patterns, either in a frontoparallel or slanted plane (±50°). One group performed a color discrimination task, while another performed a regularity discrimination task. We measured a symmetry-related event-related potential (ERP), beginning around 300 ms. During color discrimination, the ERP was reduced for slanted patterns, indexing only the remaining retinal structure. During regularity discrimination, the same ERP was view invariant, and identical for frontoparallel or slanted presentation. We conclude that normalization occurs rapidly during active symmetry discrimination, while symmetry-sensitive networks respond only to regularity in the retinal image when people are attending to other features.

Descriptors: Symmetry, Event-related potentials, Sustained posterior negativity, View invariance, Perspective distortion

The two-dimensional retinal projection of an object changes dramatically as the observer adopts different vantage points. This produces novel inputs to the recognition system, but objects are nevertheless identified reliably and rapidly, and this formidable computational feat occurs unconsciously. Logothetis and Sheinberg (1996) concluded that some neurons are view invariant (firing to their preferred stimulus independent of view angle), some are view selective (firing more for some view angles), and that view invariance is more common for familiar objects than novel objects. It is also known that the neural response to faces becomes increasingly view invariant in higher visual regions (Axelrod & Yovel, 2012). Here, we measured whether the neural response to abstract visual symmetry is view invariant or view selective.

Many visual systems are highly sensitive to symmetry, perhaps because it helps to identify objects against a background (Machilsen, Pauwels, & Wagemans, 2009), to achieve shape constancy (Pizlo & Stevenson, 1999), or because it indicates reproductive fitness (Tyler, 1995). Bilateral symmetry perception has been demonstrated in insects (Plowright, Evans, Leung, & Collin, 2011), birds (Møller, 1992), and humans (Julesz, 1971; Mach, 1886/1959). In humans, symmetry perception interacts with other figural cues (Bertamini, 2010; Treder & van der Helm, 2007), while models have been developed that extract symmetry from spatial filters (Dakin & Hess, 1997).

Most psychophysical and neuroimaging researchers have used symmetric patterns in the frontoparallel plane, which produce a symmetrical retinal projection (e.g., Bertamini, Friedenberg, & Kubovy, 1997; Jacobsen & Höfel, 2003; Makin, Pecchinenda, & Bertamini, 2012; Royer, 1981; Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005; Wenderoth, 1994). However, the benefits of symmetry perception presuppose the ability to recognize symmetrical objects from multiple viewpoints: After all, an observer will almost never encounter a symmetrical object from that privileged vantage point that results in symmetrical retinal projection. In other words, symmetrical objects in the real world would almost never activate a visual symmetry detector that is only sensitive to perfect retinal symmetry.

Although relatively understudied, there has been some excellent psychophysical work looking at symmetry detection across view angles (for review, see van der Helm, 2014). In an influential paper, Wagemans, Vangool, Swinnen, and Vanhorebeek (1993) detailed the availability of subregularities within symmetrical patterns. In the frontoparallel plane, reflection patterns are comprised of element pairs connected by invisible parallel lines and a common midpoint. There is also second-order structure, made from virtual quadrangles, which are also uniformly oriented and midpoint collinear. Skewing the patterns (which approximates a change in view angle) eliminates the second-order structures only. The authors reported that people are slower to detect skewed symmetry, possibly because informative second-order structure is removed.

In a more recent paper, van der Vloed, Csathó, and van der Helm (2005) used perspective projections rather than skewed symmetry. In their Experiment 1, participants discriminated vertical

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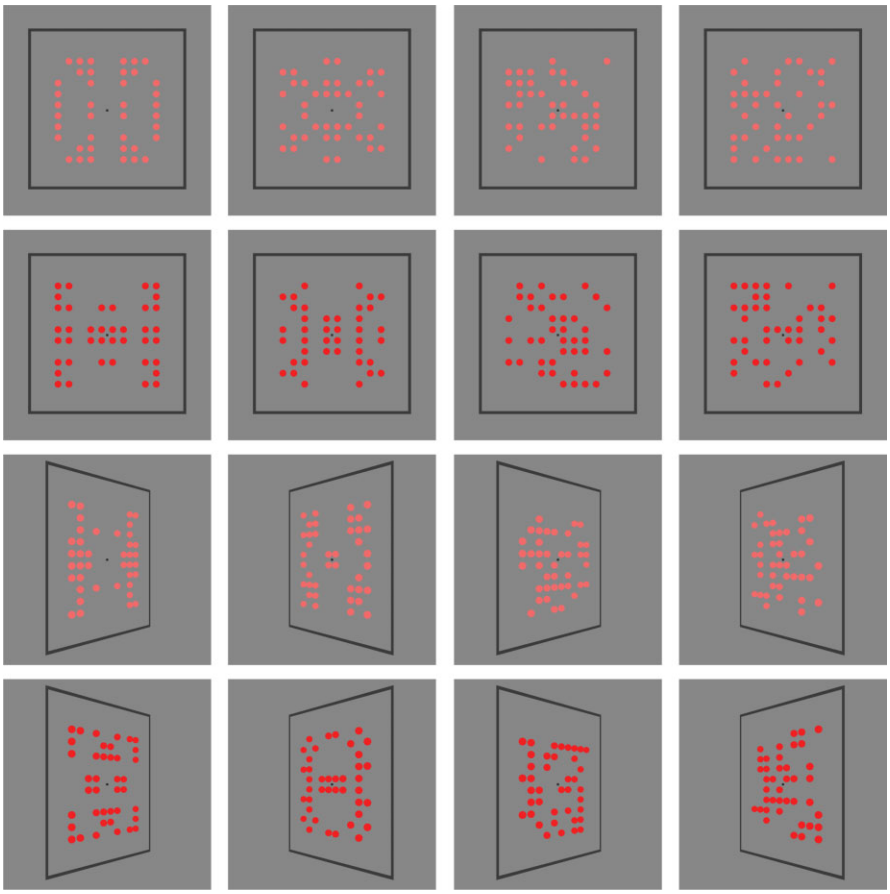

Figure 1. Example patterns from Experiment 1. This shows examples of stimuli from a 16-trial block. The experiment contained 18 such blocks, giving 288 trials in total. No two identical patterns were ever shown. Participants either discriminated regularity (reflection or random) or color (light or dark red).

reflection from random patterns. The patterns were either rotated in depth around the axis of reflection (*Y* rotation), or rotated in depth around the perpendicular axis (*X* rotation). Perspective distortions produced by *Y* rotation eliminated both first- and second-order structure. Conversely, *X* rotations eliminated neither, so retinal symmetry was preserved, despite change in view angle. Performance was parametrically impaired by increasing *Y* rotations. There were some weaker effects on detection speed for the *X* rotations that preserve retinal structure, but no effect on error rate. In their Experiment 2, participants discriminated repetition patterns from random. Unlike reflection, repetition is degraded by *X* rotations, although the damage caused by *Y* rotation is more severe. Participants were slower and less accurate when view angle increased, and were worse in the *Y* rotation condition.

The authors consider two explanations for their results. First, people may correct for perspective before discriminating symmetry. This putative normalization process could take time, hence later responses for slanted displays. This is in line with the conclusions of Szlyk, Rock, and Fisher (1995), who suggested that symmetry perception is a postconstancy process, following active normalization based on other visual cues that allow slant to be determined. A second explanation is that symmetry detection is not preceded by effortful normalization, and people perceive symmetry based on regularities available in the retinal image. If perspective slant eliminates regularities, then symmetry discrimination is impaired accordingly. After considering the results, van der Vloed et al. (2005) argued in favor of the retinal structure hypothesis, and against the normalization account. The retinal structure account captured more detail in the results, particularly the overall difference between *X* and *Y* rotations for repetition detection in their Experiment 2, which cannot be explained by the normalization account.

We return to the competing normalization and retinal structure hypotheses in our study. We recorded event-related potentials (ERP) from the scalp while people viewed symmetrical or random dot patterns from different view angles (example stimuli are shown in Figure 1).

Previous studies have reported a symmetry-related ERP known as the sustained posterior negativity (SPN): From approximately 250 ms after stimulus onset, amplitude is more negative for symmetrical than random patterns at posterior electrodes (Jacobsen & Höfel, 2003; Makin, Wilton, Pecchinenda, & Bertamini, 2012; Norcia, Candy, Pettet, Vildavski, & Tyler, 2002). The amplitude of the SPN roughly maps onto the visual salience of different regularities, although other influences are apparent as well (Makin, Rampone, Pecchinenda, & Bertamini, 2013). The SPN is present even when observers are engaged in tasks that are unrelated to stimulus regularity (Höfel & Jacobsen, 2007; Makin, Rampone, Wright, Martinovic, & Bertamini, 2014; Rampone, Makin, & Bertamini, 2014). Functional MRI (Sasaki et al., 2005) and ERP source localization techniques (Makin, Wilton et al., 2012) provide converging evidence that SPN is generated by extrastriate visual areas and by the lateral occipital

complex (LOC). We used the SPN as an index of the brain's response to symmetry.

What do the retinal structure and normalization hypotheses predict? The retinal structure hypothesis (supported by van der Vloed et al., 2005) predicts that the SPN should be reduced for the slanted presentations. Conversely, the normalization hypothesis (supported by Szlyk et al., 1995) predicts that the SPN should be the same amplitude for frontoparallel or slanted conditions, although the onset might be delayed for the slanted displays because of the extra time required for active perspective correction. Longer detection time for slanted displays is consistent with either hypothesis, whereas ERP techniques allow us to distinguish between them.

Our symmetrical patterns included reflection around two axes—horizontal and vertical. Slant was produced by rotation about the vertical axis (*Y*) through the center of the stimulus, and therefore it reduced perfect symmetry in the retinal image by 50%, with perfect reflection preserved on the *X* axis (van der Vloed et al., 2005). How much should the SPN be reduced for slanted presentations according to the retinal structure account? As a first guess, we might suppose that the brain only responds to perfect symmetry in the retinal image, and not at all to distorted symmetry. Slanting reduces perfect retinal symmetry by 50%, and could thus reduce the SPN by 50%.

However, this reasoning is based on an assumption; namely, that there is no neural response whatsoever to imperfect retinal symmetry around the depth-rotated axis. This assumption is unrealistic: It means slanted one-fold symmetry should be invisible, but people can see this when they are seeking it, even with short presentation durations (van der Vloed et al., 2005). Moreover, during passive presentation, the blood oxygen level-dependent (BOLD) response to symmetry in LOC is still present for degraded symmetry (Sasaki et al., 2005). So, even without perspective normalization, residual imperfect symmetry around the rotated axis could still activate visual regularity detectors to some degree, and generate an SPN. In summary, the retinal structure account predicts some SPN reduction when patterns are slanted, but the magnitude of this effect is not predictable from existing literature—it may be less than 50%.

Furthermore, we compared SPN in a group of 24 participants who classified patterns according to color (light red or dark red; color discrimination task) while ignoring regularity, and a group of 24 participants who classified symmetry (symmetrical or random; regularity discrimination task) while ignoring color. It is possible that the effect of slant on SPN amplitude is different in the two tasks. The normalization hypothesis is neutral with regards to when such normalization should occur; perhaps this effortful process would only be undertaken during active symmetry discrimination, and not during color discrimination, where it is not strictly necessary. Conversely, the retinal structure hypothesis implies that the SPN should always be reduced for the slanted displays.

Experiment 1

Method

Participants. Forty-eight participants were involved (aged 18 to 35, mean age 24, 19 males, 4 left-handed). All participants had normal or corrected-to-normal vision, and received £10 payment or course credit for participating. The study had local ethics committee approval and was conducted in accordance with the Declaration of Helsinki.

Apparatus. Participants sat 140 cm from a 60 Hz CRT monitor (40×30 cm). The apparatus was the same as used by Makin, Wilton et al. (2012). Electroencephalogram (EEG) data were recorded from 64 scalp electrodes at 512 Hz using the BioSemi Active-Two system, in an electrically shielded and darkened room. Additional common mode sense (CMS) and driven right leg (DRL) electrodes served as reference and ground. Bipolar horizontal and vertical electrooculograph (EOG) signals were recorded from four external channels of the BioSemi amplifier.

Stimuli. The experiment was programmed in Python using openGL and open-source PsychoPy software (Peirce, 2007). Each pattern was based on a 10×10 matrix of possible positions, filled by 40 small spheres. Around the pattern there was a gray frame that helped to specify the projection plane. Each element had a diameter of 0.3° of visual angle, and the outside frame had a side of circa 10°. In half of the trials, the elements were dark red (RGB values = 1.0, 0.6, 0.6); in the other half, they were a lighter red (RGB values = 1.0, 0.75, 0.75). Examples of stimuli are shown in Figure 1, with rows and columns organized according to condition. In the analysis, we collapse across leftward and rightward slant, but these were presented equally often. Importantly, it is possible to generate a large number of symmetrical patterns that have recognizable perceptual structure but no semantic content (Mach, 1886/1959; Makin, Pecchinenda, & Bertamini, 2012), thus avoiding the role of familiarity. For example, in our experiment 3,268,760 different symmetrical patterns are possible. Patterns were never repeated during one session, unless by remote chance.

Our patterns had two axes of symmetry, horizontal and vertical. Therefore, a single quadrant was reflected twice. Reflection patterns had 10 spheres per quadrant, while random patterns allowed the 40 spheres to appear anywhere in the four quadrants. Patterns were either presented in the frontoparallel plane or with a 50° leftwards or rightwards rotation around the vertical axis. Note that this eliminated reflectional symmetry around the vertical axis, while horizontal reflection was still present.

Design and procedure. There were 36 trials in each of eight conditions, (symmetry vs. random) × (frontoparallel vs. slanted) × (light red, dark red), giving 288 trials in total. Half of the participants performed the color discrimination task, and judged whether the elements were light red or dark red. The other half performed the regularity discrimination task, and judged whether the patterns were reflection or random. The experiment was broken into 18 blocks of 16 trials, where examples of each condition were presented twice, in a randomized order. After two blocks, participants were given an extended break and electrodes were checked.

Each trial began with a randomized 1.5 to 2 s baseline period, where participants fixated centrally on a dot. Images were presented for 1.5 s, and participants continued to fixate centrally. This was followed by a 120-ms visual noise mask to prevent afterimages. At the end of the trial, participants were prompted to press either the Z (left) or / (right) keys on a standard computer keyboard, to report whether the image was symmetrical or random (regularity discrimination task) or whether the items were light or dark red (color discrimination task). The response mappings were unpredictable on each trial, to prevent motor readiness potentials during the period when the stimulus was displayed (see Makin et al., 2013, for details).

Analysis. EEG data was processed with EEGLAB toolbox for MATLAB (Delorme & Makeig, 2004). Raw EEG data were rereferenced to a scalp average, low-pass filtered at 25 Hz, and

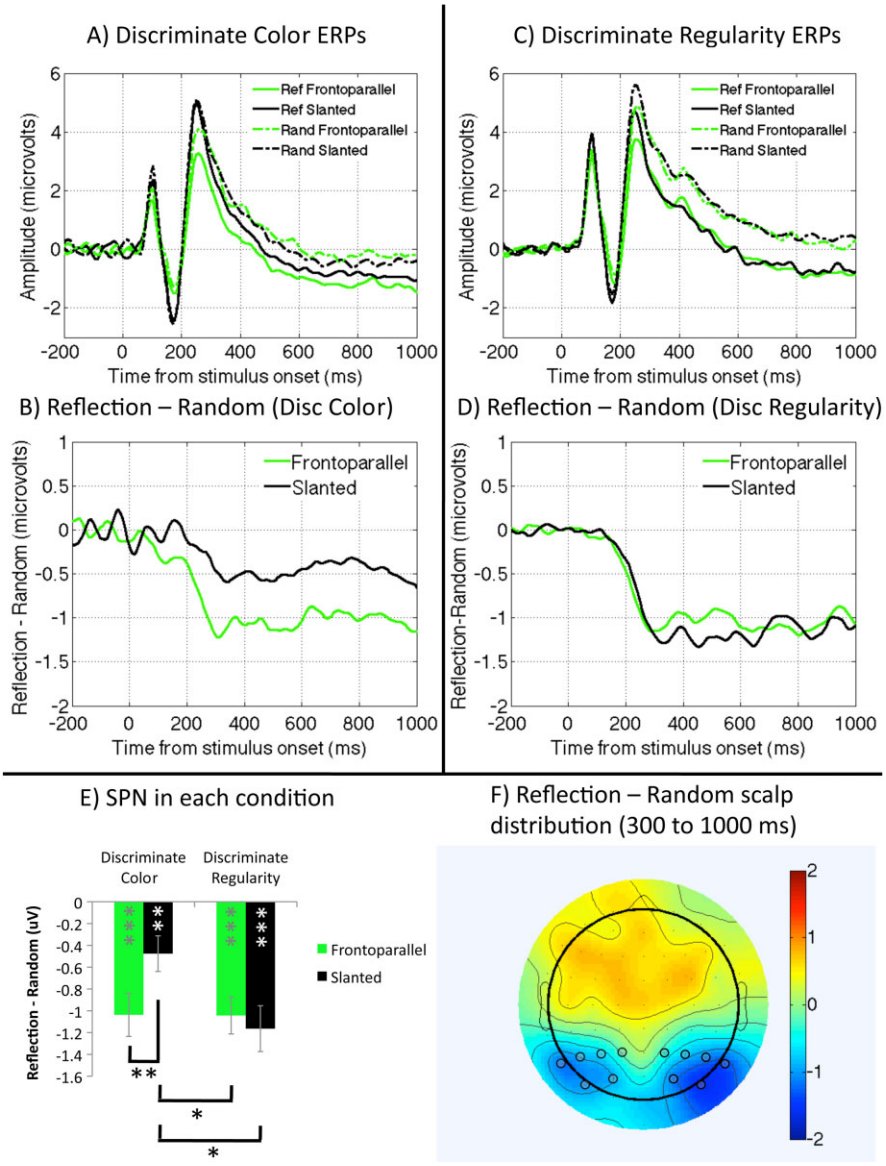

Figure 2. Experiment 1 results. A: Grand-average ERP waves from posterior electrode clusters for the group of participants discriminating color. B: Grand-average reflection–random difference waves in the frontoparallel and slanted conditions of the color discrimination task. C: Grand-average ERPs from participants discriminating regularity. D: Difference waves from regularity discrimination task. E: SPN component in each condition (reflection–random amplitude, from 300 ms to 1,000 ms, poststimulus onset). Asterisks within the bars indicate the difference from zero (i.e., reflection < random); others indicate difference between conditions (*$p < .05$; **$p < .01$; ***$p < .001$). Error bars = ± 1 *SEM*. F: Grand-average scalp map showing the topography of the SPN component (collapsed across all other conditions). Electrodes used for analysis are highlighted.

downsampled to 128 Hz to reduce file size. The data were then epoched into −1 to 1.5 s epochs, with a −200 ms to 0 baseline. Blinks, eye movement, and other gross artifacts were removed with independent component analysis (ICA, mean components removed = 11.35). After ICA, epochs were rejected if amplitude exceeded ± 100 µV (~9% in each condition). Trials within a condition were averaged for each participant, and grand-average ERPs were obtained (see Makin et al., 2013, for example of comparable data treatment). The SPN was defined as lower amplitude for symmetrical than random patterns from 300 to 1,000 ms, averaged across left and right posterior electrodes (P1, P3, P5, P7, PO3, PO7 on the left, and P2, P4, P6, P8, PO4, and PO8 on the right; Figure 2F). The time window was chosen for consistency with previous studies (Makin et al., 2013; Makin, Wilton et al., 2012). Effect sizes are reported after significant results (η_p^2, which gives proportion of variance explained by a factor in analysis of variance [ANOVA], or Cohen's d_z, the difference between paired means in *SD* units, or Cohen's d_s, which gives difference between group means in *SD* units).

Results

Behavioral results. One group of participants discriminated reflection from random patterns, another group discriminated light from dark red dots. Performance was near perfect in both groups of participants, with an average of 96% correct in the color

discrimination task, and 97% correct in the regularity discrimination task, $t(23) = 0.321$, $p = .751$.

EEG results. In all conditions, we recorded an SPN component at posterior electrode clusters. The scalp distribution of the SPN is shown in Figure 2F. The posterior electrodes used for SPN analysis are highlighted with small dots (P1, P3, P5, P7, PO3, PO7, and right-sided homologues). The ERPs from each condition are shown in Figures 2A–D. Figure 2A shows ERP from posterior electrodes from the color discrimination task. There was an orderly P1-N1-P2 response, which is germane to all visual onsets. After this, there was a prolonged period where amplitude is lower in reflection than random trials (the SPN). The SPN is clearer in Figure 2B, which shows the reflection-random difference wave in the frontoparallel and slanted conditions of the color discrimination task. Negative values indicate lower amplitude for reflection. Note that the SPN was approximately twice the size for frontoparallel presentations (~1 μV) compared to slanted presentations (~0.5 μV). This is a clear example of a view-selective response. Figure 2C,D shows equivalent data from the regularity discrimination task. The SPN was now identical in frontoparallel and slanted conditions (~1 μV in both). This is a view-invariant response.

The SPN was analyzed with mixed ANOVAs with two within-subjects factors, Regularity (reflection, random) × Angle (frontoparallel, slanted), and one between-subjects factor, task (color discrimination, regularity discrimination). There was a strong main effect of regularity, $F(1,46) = 76.558$, $p < .001$, $\eta_p^2 = .625$. The only other significant effect was the three-way interaction, Regularity × Angle × Task, $F(1,46) = 4.772$, $p = .034$, $\eta_p^2 = .094$. This interaction was followed up with paired samples *t* tests.

In the color discrimination task, there was an SPN in both the frontoparallel condition, $t(23) = 5.215$, $p < .001$, $d_z = 1.065$, and the slanted condition, $t(23) = 2.908$, $p = .008$, $d_z = 0.594$. However, amplitude was significantly reduced in slanted displays, $t(23) = 3.655$, $p = .001$, $d_z = 0.764$. Conversely, for the group of participants who were classifying patterns by regularity, the SPN was similar in frontoparallel and slanted conditions, $t(23) = 0.444$, $p = .661$, and significant for both (frontoparallel, $t(23) = 6.153$, $p < .001$ $d_z = 1.256$; slanted, $t(23) = 5.543$, $p < .001$, $d_z = 1.131$). The same results can be described as follows: When patterns were frontoparallel, the SPN was nearly identical when participants were discriminating color or regularity, $t(46) = 0.024$, $p = .981$ (green/gray lines in Figure 2B,D). Conversely, when the patterns were slanted, the SPN was significantly reduced in the color discrimination group, $t(46) = 2.587$, $p = .013$, $d_s = 0.747$ (black lines in Figure 2B,D). These effects can also be seen in Figure 2E, where bars represent SPN amplitude in the different conditions.

Discussion

As with previous studies, an ERP called the sustained posterior negativity reliably distinguished between reflection and random patterns (Höfel & Jacobsen, 2007; Jacobsen & Höfel, 2003; Makin et al., 2013, 2014; Makin, Wilton et al., 2012; Norcia et al., 2002). When participants discriminated regularity, the SPN was view invariant: It was the same whether patterns were in the frontoparallel plane or in the slanted plane. Conversely, when participants were discriminating color, the SPN was view selective: It was present, but significantly reduced, in the slanted displays.

We conclude that, in the color discrimination task, regularity detectors in the extrastriate visual cortex only respond to the regularity in the retinal image, not regularity in the distal object. When regularity was reduced substantially by perspective slant, the SPN was reduced accordingly. More precisely: halving the regularity in the retinal image halved the amplitude of the SPN. This reduction is surprisingly large; it implies that there was no response at all to the degraded regularity around the vertical axis in the slant condition, while previous work suggests that the brain responds to imperfect symmetry, even when attention is directed to other stimulus features (Sasaki et al., 2005).

Experiment 2

Experiment 1 suggested that, when attention is directed to other features, regularity detectors only respond to perfect retinal structure. Experiment 2 replicated the color discrimination task from Experiment 1, but included only a single axis of reflection. Now, perspective slant eliminates perfect retinal structure completely, as shown in Figure 3A. A strong prediction for Experiment 2 is that the SPN will be around 0.5 μV in the frontoparallel condition, and be reduced to near zero in the slanted condition. The results of Experiment 2 were analyzed together with the color discrimination task of Experiment 1 to test this prediction statistically.

Method

Another group of 24 participants were involved (age 15 to 41, 11 male, all right-handed). All participants had normal or corrected-to-normal vision, and some received £10 payment. The apparatus and procedure were identical to the color discrimination task of Experiment 1 with the exception that reflection involved only a single vertical axis (Figure 3A). We kept the preprocessing stages and electrode selection identical to Experiment 1 to facilitate comparison. An average of 10.25 components were removed with ICA (min = 3, max = 17). After ICA, epochs were rejected if amplitude exceeded ± 100 μV (~3–4% in each condition). Consequences of alternative preprocessing decisions are explored in the Control Analysis section below.

Results

Participants discriminated light from dark red patterns accurately in 96% of the trials. SPN difference waves are shown Figure 3B, alongside those of the color discrimination task from Experiment 1. The most important finding was that the SPN was approximately proportional to amount of retinal structure in the display: Two-fold frontoparallel reflections produced a 1 μV SPN. Two-fold slanted and one-fold frontoparallel (i.e., both one axis of retinal symmetry) both produce a 0.5 μV SPN. Finally, one-fold slanted reflections (with no retinal symmetry) produced no significant SPN (although a small effect was apparent). We can (roughly) summarize by saying that addition of each new axis of retinal symmetry adds approximately 0.5 μV to the SPN. This is seen in Figure 3C, where SPN amplitude is shown as a function of the number of retinal reflections in the display. Here, we see the linear relationship between the variables ($r^2 = .94$). Figure 3D, on the other hand, shows SPN amplitude as a function of reflections in the distal object. This relationship is much weaker ($r^2 = .51$), supporting our claim that, when people are engaged in color discrimination, their SPN generators respond to retinal structure only.

These results were analyzed with three-factor mixed ANOVAs, with two within-subjects factors, Regularity (reflection, random) × Angle (frontoparallel, slanted), and one

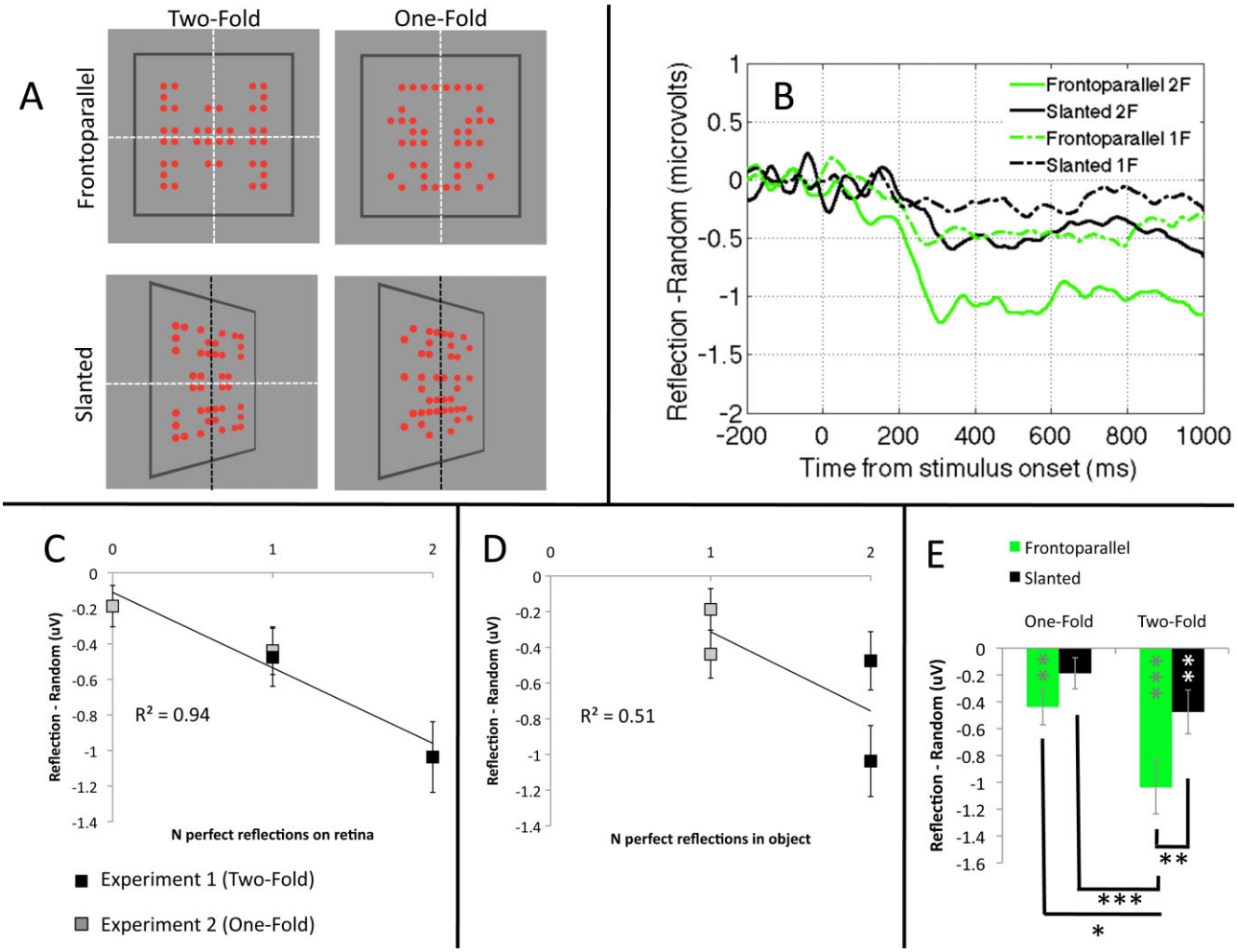

Figure 3. Experiment 2 results. A: Axes in the frontoparallel and slanted reflection patterns, with one- or two-fold patterns. White dotted lines indicate retinal structure; black dotted lines indicate additional reflections in the distal object. B: Reflection–random difference waves in color discrimination tasks with one- and two-fold patterns (1F from Experiment 2 participants, 2F from Experiment 1 participants). C: SPN amplitude plotted against the number of perfect axes of reflection in the retinal image. D: Same data plotted against axes of reflection in the distal pattern, independent of view angle. E: Statistical analysis of the SPN from color discrimination tasks.

between-subjects factor, folds (one, two). There was a main effect of regularity, $F(1,46) = 30.468$, $p < .001$, $\eta_p^2 = .398$, which was modulated by the between-subjects factor, folds, $F(1,46) = 5.241$, $p = .027$, $\eta_p^2 = .101$. In addition, there was Regularity × Angle interaction, $F(1,46) = 14.475$, $p < .001$, $\eta_p^2 = .239$. There were no other effects or interactions: max $F(1,46) = 2.655$, $p > .110$.

Significant paired comparisons are shown in Figure 3E. There was a significant SPN in the one-fold frontoparallel condition, $t(23) = 3.264$, $p = .003$, $d_z = 0.666$. The two-fold frontoparallel SPN in Experiment 1 was significantly greater than both the SPNs recorded in Experiment 2 (frontoparallel, $t(46) = 2.495$, $p = .016$, $d_s = 0.720$; slanted, $t(46) = 3.689$, $p = .001$, $d_s = 1.065$). Two noteworthy null effects here were the unique absence of an SPN in the one-fold slanted condition, $t(23) = -1.612$, $p = .120$), and the absence of a difference between frontoparallel one-fold and slanted two-fold, $t(46) = 0.176$, $p = .861$.

Discussion

Combined analysis of color discrimination tasks from Experiments 1 and 2 strengthens the conclusions of Experiment 1. We propose that, during color discrimination tasks, the addition of an axis of reflection to the retinal image increases the amplitude of the SPN by approximately 0.5 μV, while distorted regularity remaining after slant makes no contribution. In the next section, we consider some important caveats to this simple story.

The findings of our color discrimination tasks are not without precedent. Oka, Victor, Conte, & Yanagida (2007) used steady state visual evoked potential technique, and found a correlation between the number of reflection axes in the stimuli and the size of the driven neural response to symmetry during passive viewing. The results of our color discrimination task mirror these findings, using traditional ERPs.

The link between this work and other literature is less straightforward: Makin et al. (2013) concluded that the amplitude of the SPN maps the salience of different regularities, reflection, rotation, and repetition, where salience is indexed by performance in psychophysical regularity detection tasks. Meanwhile, van der Vloed et al. (2005) found that repetition detection was much worse than reflection detection (even when comparing frontoparallel repetition with 60° slanted reflections). According to the salience

account, we would expect the SPN reduction for slant reflection to be much less than SPN reduction for repetition, but comparison of the current results with those of Makin et al. (2013) do not support this. In fact, the SPN reduction for repetition in Makin et al. (2013) was approximately the same as the SPN reduction for slant reported here. We thus conclude that it is currently impossible to link psychophysical data on salience of different regularities with SPN effects, especially when the stimuli, tasks, and participants are not matched.

Control Analysis

The most important effect in the current experiment was the ~50% reduction of SPN amplitude in the slanted conditions of the color discrimination task, and the further SPN reductions in Experiment 2, where one-fold patterns were presented. We reasoned that reduction of grand-average SPN could be produced in two distinct ways: (1) a comparable SPN reduction in all participants, or (2) complete disappearance of the SPN in half the participants, but no reduction of SPN in the others. Nonparametric analysis supported the first hypothesis. In the color discrimination task of Experiment 1, the SPN (reflection < random) was present in 20/24 ($p = .002$, binomial test) participants for the frontoparallel condition, and 19/24 participants for the slanted condition ($p = .007$). In Experiment 2, the SPN was present in 19/24 participants for frontoparallel ($p = .007$), but was only present in around 13/24 of participants for slanted ($p = .839$). Therefore, we can conclude that, whenever the grand-average SPN is present but reduced, this is not due to reduction in the number of participants that show the effect.

The between-subjects design had the advantage of avoiding order effects, but also some disadvantages. The group of participants in the color discrimination task of Experiment 1 were significantly older than those in the regularity discrimination task (mean age 31 vs. 23; $t(46) = 2.666$, $p = .011$, $d_s = 0.770$). Older participants could be worse at perspective correction, resulting in reduced response to slanted symmetry. However, we found no evidence that participant age was systematically correlated with SPN amplitude in slanted conditions (color discrimination two-fold, $r = .177$, $p = .407$; regularity discrimination, $r = .101$, $p = .607$; color discrimination one-fold, $r = .148$, $p = .491$), so the age confound is very unlikely to explain the results. Samples in color and regularity tasks of Experiment 1 did not differ significantly in terms of gender (13 vs. 6 males, $p = .167$) or handedness (1 vs. 3 left-handed, $p = .625$), and there were no differences between the samples used in color discrimination tasks of Experiments 1 and 2 (mean age 31 vs. 25, $t(46) = 1.817$, $p = .076$; 1 vs. 0 left-handed; 13 vs. 11 males, $p = 0.839$).

Next, we consider the interrelations between amplitude and topography. The electrodes for analysis were based on the topographic difference map shown in Figure 2F, which averaged overall conditions of Experiment 1. Figure 4 shows the same information for each condition of Experiments 1 and 2. It can be seen here that there is some relationship between the amplitude of the SPN and the size of the electrode clusters that capture the effect.

In order to measure effects on amplitude independently from topography, we reanalyzed the SPN using PO7 and PO8 only (highlighted red in Figure 4). The results from Experiment 1 were essentially the same with this analysis: There was still a three-way interaction, Regularity × Angle × Task, $F(1,46) = 4.480$, $p = .040$, $\eta_p^2 = .089$. In the regularity discrimination task, the main effect of regularity, $F(1,23) = 91.935$, $p < .001$, $\eta_p^2 = .800$, did not interact with angle, $F(1,23) < 1$, *n.s.*, while in the color discrimination task, there was a main effect of regularity, $F(1,23) = 6.250$, $p = .020$, $\eta_p^2 = .214$, which was further modulated by angle, $F(1,23) = 5.899$, $p = .023$, $\eta_p^2 = .204$. The combined analysis of color discrimination tasks produces an important difference: There was again a main effect of regularity, $F(1,46) = 16.385$, $p < .001$, $\eta_p^2 = .263$; however, unlike the analysis based on the full clusters, this did not significantly interact with folds, $F(1,46) < 1$, *n.s.* SPN reduction in Experiment 2 thus reflects restricted topography, as well as reduced amplitude. The important Regularity × Angle interaction was still present in PO7/PO8, $F(1,46) = 5.783$, $p = .020$, $\eta_p^2 = .112$.

Topographic maps suggest that SPN was larger in the right posterior electrodes. To explore this, we reanalyzed the posterior ERP from Experiment 1 with hemisphere (left, right) as an additional factor. The apparent lateralization in Figure 2F was supported by a Hemisphere × Regularity interaction, $F(1,46) = 4.720$, $p = .035$, $\eta_p^2 = .093$. Although stronger on the right, the effect of regularity was significant in both hemispheres, left: $F(1,46) = 41.454$, $p < .001$, $\eta_p^2 = 0.474$; right: $F(1,46) = 86.649$, $p < .001$, $\eta_p^2 = .653$. The only other effect including the factor hemisphere was a three-way interaction, Hemisphere × Angle × Experiment, $F(1,46) = 9.414$, $p = .004$, $\eta_p^2 = .170$. This reflects a combination of intricate effects that we do not elaborate on here. Crucially, the important three-way interaction between regularity, angle, and task did not significantly differ between hemispheres, $F(1,46) < 1$, *n.s.*

Next, we repeated the combined analysis of color discrimination tasks with hemisphere as an additional factor. There was no Hemisphere × Regularity interaction here, $F(1,46) = 1.639$, $p = .207$, suggesting that the SPN was bilateral in our color discrimination tasks. There was a three-way interaction between hemisphere, regularity, and angle, $F(1,46) = 8.494$, $p = .005$, $\eta_p^2 = 0.156$. The Regularity × Angle interaction was not significant on the left, $F(1,46) = 1.153$, $p = .289$, but was very strong on the right, $F(1,46) = 23.170$, $p < .001$, $\eta_p^2 = .335$.

Additional analysis explored correlations of SPN amplitude between hemispheres. A positive correlation was found in all three groups of participants (color discrimination two-fold, $r = .62$, $p = .001$, regularity discrimination, $r = .55$, $p = .006$; color discrimination one-fold, $r = .63$, $p = .001$). From this, we conclude that individual differences in symmetry sensitivity tend to be bilateral.

We then moved on to test whether the neural response to symmetry interacted with the ERPs generated by pattern color. (Note that the light and dark red patterns were not luminance matched: we thus use the word color as shorthand for a factor in the experimental design—any ERP effects could equally be due to luminance). Dark red patterns also produced a sustained negativity at electrodes over the visual cortex. However, unlike the symmetry-related SPN, this component had central rather than bilateral topographic focus. This difference can be seen by comparing scalp maps in Figure 5A (reflection–random) and Figure 5C (dark red–light red). Crucially, the two ERPs did not interact, indicating that the neural responses to color and symmetry were independent. Electrodes used for difference waves and analyses are highlighted in the topographic maps. The reflection–random difference waves in light and dark red conditions are shown in Figure 5B. This size of response differed between tasks, as discussed above. Importantly, this SPN was very similar in light and dark conditions. The dark–light difference wave are shown in Figure 5D. Here, we see the same response to color across tasks, and that this was not altered by regularity.

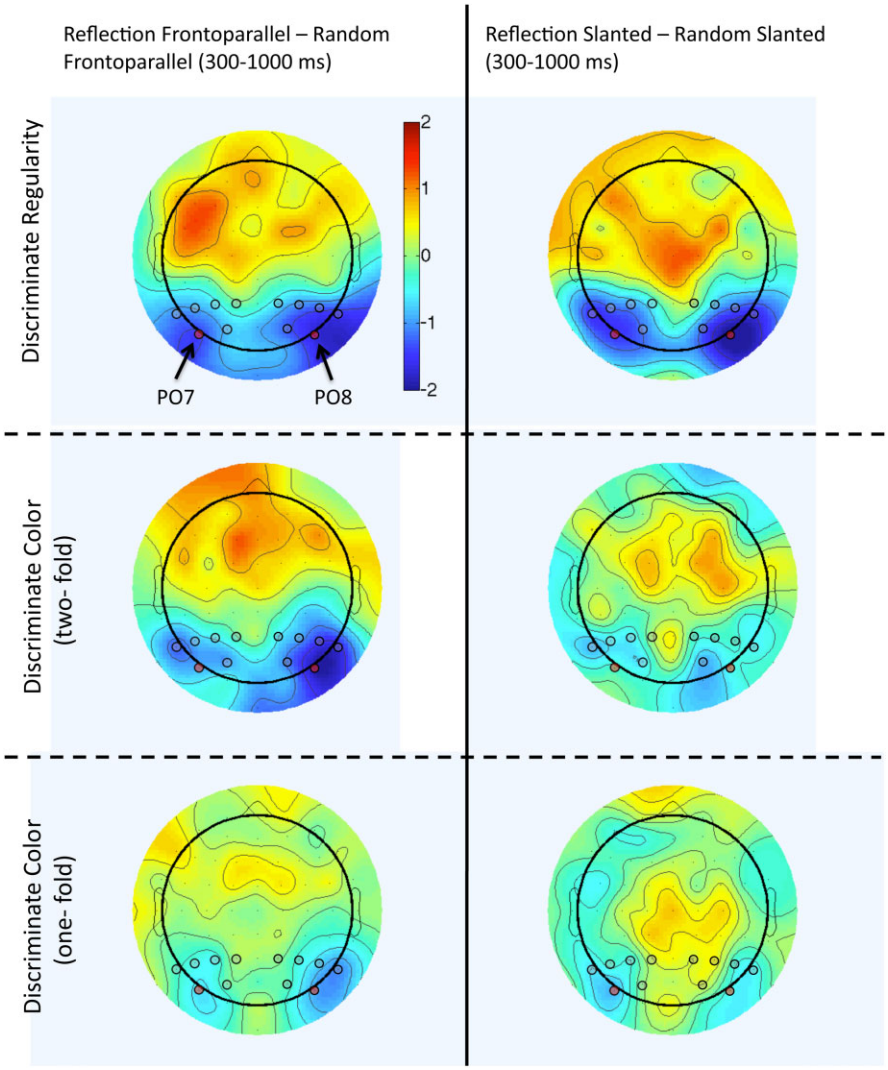

Figure 4. Reflection–random topographic plots. Columns show frontoparallel and slanted conditions. Rows show results from groups of subjects involved in the separate tasks. Electrode clusters used for most analyses are highlighted gray. The PO7 and PO8 electrodes, used for control analysis, are highlighted.

The symmetry-related SPN (quantified as reflection–random; Figure 5B) was analyzed with a single within-subject factor, color (light red, dark red) and a single between-subjects factor, task, (regularity discrimination, color discrimination two-fold, color discrimination one-fold). The SPN differed between tasks, $F(2,69) = 8.423$, $p = .001$, $\eta_p^2 = .196$. However, there was no effect of color, $F(1,69) < 1$, *n.s.* and no Task × Color interaction, $F(2,69) = 1.460$, $p = .239$.

Next, the color difference waves (quantified as dark–light; Figure 5D) were analyzed with a single within-subjects factor, regularity (reflection, random), and a single between-subjects factor, task, (regularity discrimination, color discrimination two-fold, color discrimination one-fold). There were no effects or interactions (max $F(2,69) = 1.923$, $p = .154$). In summary, this analysis supports the conclusion that regularity and color are processed by entirely separate mechanisms, resulting in independent ERPs.

Further analysis of the color difference waves showed that this response was largely independent of angle. The color difference wave was reanalyzed with a single within-subjects factor, angle (frontoparallel, slanted), and a single between-subjects factor, task (regularity discrimination, color discrimination two-fold, color discrimination one-fold). There were no effects or interactions (max $F(2,69) = 1.983$, $p = .145$).

Participants were instructed to fixate and avoid blinking, and analysis procedures were designed to remove eye movement artifacts from the EEG data. Nevertheless, ocular artifacts (or side effects of correction procedures) could still have contaminated the ERP recordings. We thus measured EOG signals to explore the prevalence of eye movements. We improved on the EOG analysis techniques used in our previous studies (e.g., Makin et al., 2013) by measuring EOG activity at the time window of the SPN only, and only for trials included in the ERP analysis. For the selected EOG data, we computed the difference between maximum and minimum amplitude, then averaged this metric over all trials in each condition.

Vertical (VEOG) and horizontal (HEOG) EOG activity were explored with separate three-factor mixed ANOVAs. For VEOG, there were no effects or interactions, max $F(1,69) = 2.832$, $p = .097$, suggesting that blinks were evenly distributed across conditions (Figure 6A). HEOG results are shown in Figure 6B. There

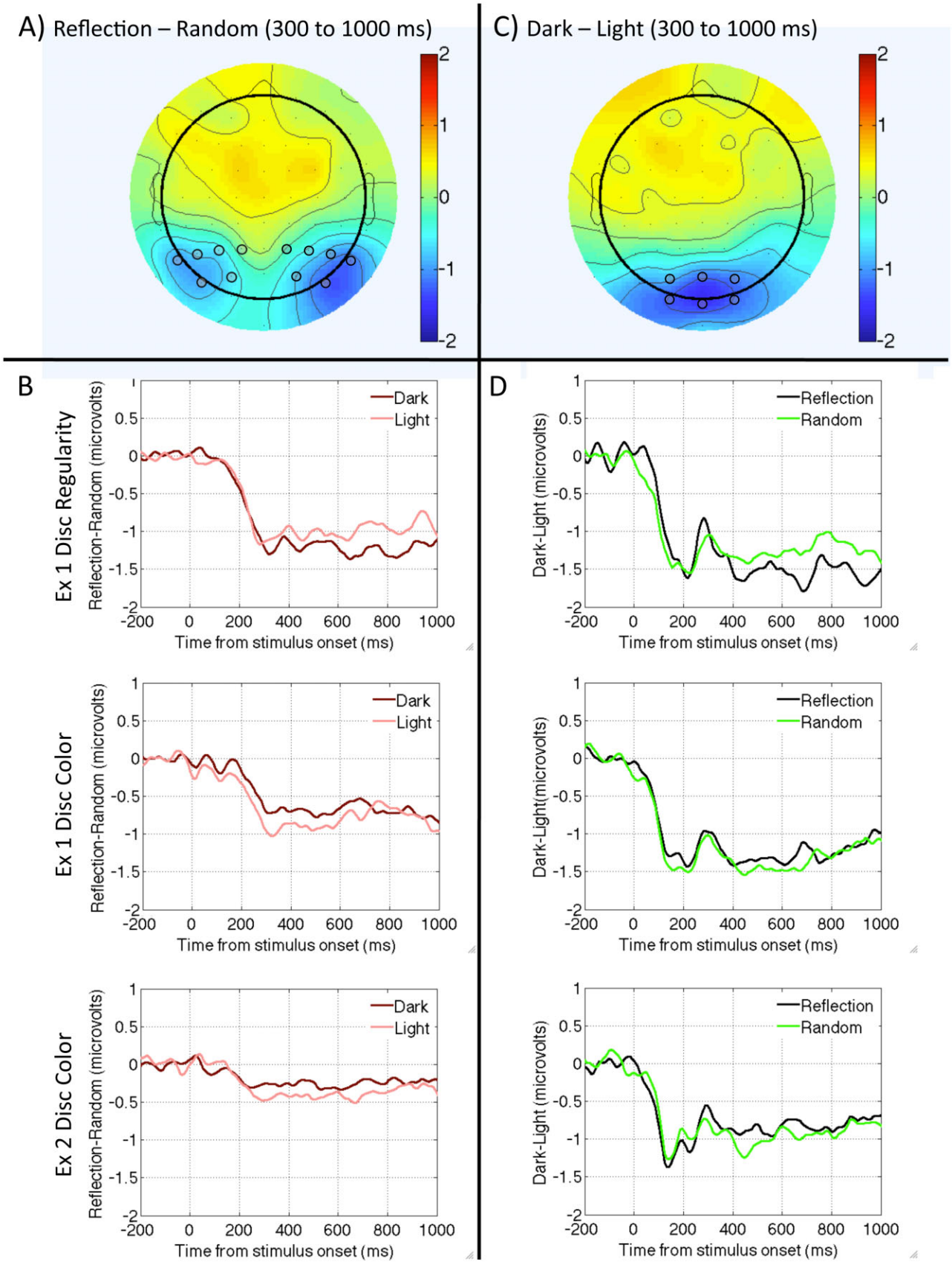

Figure 5. Independence of regularity and color ERPs. A: Reflection–random difference plot (averaged across all conditions). B: Regularity difference waves in the dark and light red conditions of each task. C: Dark–light topographic plot (averaged across all conditions). D: Color difference waves in the reflection and random conditions of each task.

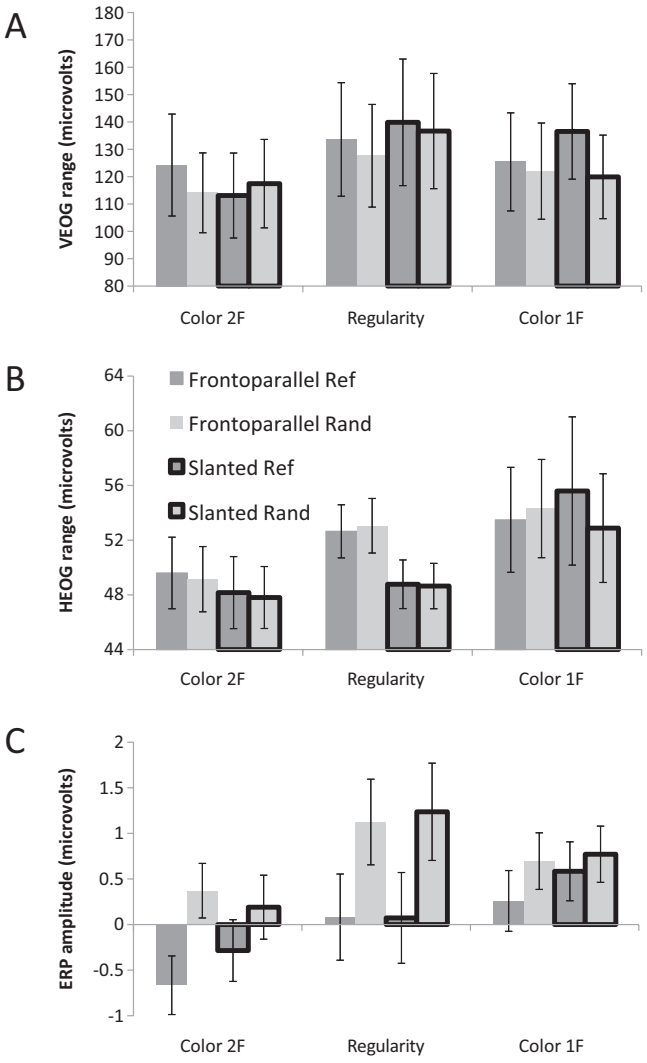

Figure 6. Oculomotor artifacts. A: VEOG range in all conditions. B: HEOG in all conditions. C: Posterior ERP amplitude in all conditions. Error bars = ± 1 *SEM*.

was a main effect of angle, because HEOG activity was higher for frontoparallel images, $F(1,69) = 7.460$, $p = .008$, $\eta_p^2 = .098$. There was also an Angle × Task interaction, $F(2,69) = 4.244$, $p = .018$, $\eta_p^2 = .110$, because the main effect of angle was significant in the regularity discrimination task, $F(1,23) = 22.006$, $p < .001$, $\eta_p^2 = .489$, but not in the color discrimination tasks of Experiment 1, $F(1,23) = 2.821$, $p = .107$, or Experiment 2, $F(1,23) < 1$, *n.s.* These HEOG effects are worth considering, but are not of serious concern: The pattern was very different from the ERPs at posterior electrodes (shown in Figure 4C for comparison). Furthermore, the amplitude of the mean HEOG signal varied between participants (29 to 154 μV), but this did not correlate with the amplitude of their posterior ERPs in any condition (max $r = .264$, $p = .213$). We are thus confident that the crucial SPN results are not an artifact of systematic eye movement differences between the conditions.

General Discussion

Previous work has shown that symmetry discrimination is delayed when patterns are viewed from an angle that destroys regularity in the retinal image. What explains this delay? It could be that symmetry discrimination follows an active perspective-normalization process, where other cues are used to achieve perceptual constancy prior to symmetry discrimination (Szlyk et al., 1995). This normalization takes time, hence systematically slowed symmetry discrimination. Alternatively, symmetry discrimination may proceed without normalization, based only upon the remaining regularity in the retinal image (van der Vloed et al., 2005). Our results show that both accounts are correct, but within different contexts. The normalization account explains the SPN data from the regularity discrimination task, while the retinal structure account fits the SPN results from the color discrimination tasks. It seems that normalization occurs when it is task relevant, while analysis of residual regularity in the retinal image proceeds automatically even when the observer is attending to other features.

First, let us consider the regularity discrimination task of Experiment 1, where the SPN was near identical for patterns seen in the frontoparallel or in the slanted planes. As mentioned above, Wagemans et al. (1993) described first- and second-order regularities in symmetrical patterns. If the pattern has a single reflection axis, both regularities can be eliminated by a perspective distortion. However, with double-axis symmetry, both kinds of regularity are preserved along the axis that is orthogonal to the slant. The retinal structures hypothesis of van der Vloed et al. (2005) predicts that SPN amplitude should be reduced in the slanted condition. However, there was no hint of this in the regularity discrimination task. The results thus suggest that perspective normalization was achieved prior to symmetry discrimination, and the brain's symmetry detectors responded equivalently to symmetry when viewed from any angle.

Next, consider the results of the color discrimination task of Experiment 1. Now, SPN amplitude was approximately halved in the slanted displays. It seems that normalization did not occur in the color discrimination task, and the brain's symmetry detectors responded to the remaining regularity in the retinal image. As discussed, the SPN slant reduction was surprisingly large: it suggests that there was no response to the residual distorted regularity around the *Y* axis. This seems superficially inconsistent with the results of Sasaki et al. (2005), where some neural response to imperfect symmetry was found during an orthogonal discrimination task. However, the symmetrical Julesz-style dot stimuli used by Sasaki et al. (2005) always contained some perfect retinal structure (although the proportion of structure to noise was varied). This contrasts with reflection around a depth-rotated *Y* axis, which contains no perfect regularity.

It is also instructive that SPN amplitude was not reduced at all in the frontoparallel displays of the color discrimination task (the SPN in the frontoparallel condition of the color discrimination task was very similar to the SPN in both conditions of the regularity discrimination task). This shows that neural response to symmetry is not uniformly inhibited during color discrimination. In the color discrimination task, it seems that the brain abandoned the perspective normalization process altogether, while regularity detection (based on whatever retinal structure was present) remained intact.

Finally, consider the results of Experiment 2, which replicated the color discrimination task, using only a single vertical axis. We began with the hypothesis that the brain only responds to retinal structure during color discrimination. We predicted that the SPN difference wave would be reduced from ~1 μV to around 0.5 μV in the frontoparallel conditions here, and to 0 μV in the slanted conditions (which have no perfect regularity). These predictions were broadly confirmed, although control analysis showed that the SPN

reduction results from restricted topography as well as reduced amplitude (see Control Analysis and Figure 4).

In summary, we show that symmetry perception can be either view invariant or view selective, depending on whether people are actively discriminating symmetry or not. Some additional perceptual work is required to correct for the slant (perhaps exploiting picture plane information in the frame or other cues; Vishwanath, Girshick, & Banks, 2005). It would waste neural resources to undertake slant correction unnecessarily, and indeed our results show that slant correction is absent when discriminating color.

We also note that when slant correction was useful in the regularity discrimination task, it proceeded without significant delay: The SPN began at approximately the same time in the frontoparallel and slanted conditions. This similarity is not consistent with an effortful mental rotation of the virtual picture (e.g., Cutting, 1987; Shepard & Metzler, 1971) as this would delay SPN onset. Instead, it seems that perspective correction for view angle was achieved very rapidly, perhaps within the first 250 ms after the pattern was presented, and this did not delay SPN considerably.

Why have previous psychophysical experiments found impaired symmetry discrimination performance for slanted presentations (e.g., van der Vloed et al., 2005; Wagemans et al., 1993), while the neural response to symmetry was identical across view angles in our regularity discrimination task? We think it is likely that the frame provided a strong perspective cue in our experiment, which meant that perspective normalization was very efficient when required. In support of this interpretation, the detrimental effects of slant on accuracy were reduced in van der Vloed's (2005) blob condition, where an implicit frame was visible around the pattern elements. However, there was still a systematic effect of slant on reaction time in the blob condition, so further explanation is required. Future ERP studies could use slanted patterns that have been demonstrated to delay regularity discrimination. We anticipate the SPN could be delayed when such stimuli are used.

Previous fMRI work has measured hemodynamic changes while people viewed symmetrical or random patterns. Sasaki et al. (2005) found symmetry-related activations in several extrastriate areas, from V3a to V7 and the LOC. Tyler et al. (2005) and Chen, Kao, and Tyler (2007) also reported symmetry activations more specific to the LOC, while other research has found that symmetry perception could be disrupted by transcranial magnetic stimulation applied to the LOC (Cattaneo, Mattavelli, Papagno, Herbert, & Silvanto, 2011). Makin, Wilton et al. (2012) tentatively suggested that LOC activation generates the SPN, based on source localization and the above literature. Interestingly, Kourtzi and Kanwisher (2001) found evidence for object-centric coding in the LOC using fMRI. However, the current results imply that the LOC response to symmetry is not always object-centric, but can become so when necessary.

It is known that increasing familiarity with objects can produce view-invariant coding (Logothetis & Sheinberg, 1996), which may arise when multiple view-dependent representations have accumulated (Vetter, Poggio, & Bulthoff, 1994). Although the same pattern was never shown twice in our experiment, and only three view angles were included (0° and ± 50° depth rotations), our stimuli were sufficient to produce view invariance in the regularity discrimination task, but not sufficient to produce automatic view invariance in the color discrimination tasks. Future work could test exposure to multiple depth-rotation increments to ascertain whether this leads to automatic view invariance (i.e., demonstrated by identical SPN across view angles during color discrimination). This reasoning implies that view invariance for symmetry must be learned through perceptual experience. If so, the brain must be preorganized from birth to facilitate the acquisition of this ability, as view-invariant responses to symmetry can be trained in 3-day-old poultry chicks (Mascalzoni, Osorio, Regolin, & Vallortigara, 2012).

Conclusion

In the symmetry perception literature, there is debate about the origins of slowed detection speed for slanted presentations. This can be attributed to either (a) time-consuming normalization, or (b) reduced retinal structure. We used symmetry-sensitive ERPs to answer this question. We recorded a view-invariant neural response to symmetry during a regularity discrimination task, but a systematically reduced response to slanted symmetry during two color discrimination tasks. We tentatively conclude that the normalization account describes active symmetry discrimination, while the retinal structure account describes symmetry perception when people are attending to other features. This is probably the more common scenario outside the lab, when people are rarely engaged in active symmetry discrimination.

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